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FUTURE DIRECTIONS No. 4

A conceptual framework for predicting the effects of urban environments on floras

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Summary

1. With the majority of people now living in urban environments, urbanization is arguably the most intensive and irreversible ecosystem change on the planet.
2. Urbanization transforms floras through a series of filters that change: (i) habitat availability; (ii) the spatial arrangement of habitats; (iii) the pool of plant species; and (iv) evolutionary selection pressures on populations persisting in the urban environment.
3. Using a framework based on mechanisms of change leads to specific predictions of floristic change in urban environments. Explicitly linking drivers of floristic change to predicted outcomes in urban areas can facilitate sustainable management of urban vegetation as well as the conservation of biodiversity.
4. *Synthesis*. We outline how the use of our proposed framework, based on environmental filtering, can be used to predict responses of floras to urbanization. These floristic responses can be assessed using metrics of taxonomic composition, phylogenetic relatedness among species, plant trait distributions or plant community structure. We outline how this framework can be applied to studies that compare floras within cities or among cities to better understand the various floristic responses to urbanization.

Key-words: community phylogenetics, extinction, fragmentation, habitat loss, invasion, plant traits, selection, stress, sustainability, urbanization

Urban environments, including cities, suburbs, peri-urban areas and towns, rely on vegetation to provide ecosystem functions such as air filtering, temperature amelioration, and water storage, filtration and drainage (Bolund & Hunhammar 1999). The vegetation of urban areas has societal value in defining nature for millions of people living in cities and sustaining public health and well-being (Ulrich 1984; Kuo & Sullivan 2001; Fuller *et al.* 2007), as well as often contributing to the conservation estate by supporting unique biodiversity (McDowell *et al.* 1991; Schwartz *et al.* 2002; Lawson *et al.* 2008). Thus, the urban environment provides a unique opportunity to meld ecological management with landscape design to provide a variety of societal goods and services (Pickett & Cadenasso 2008). Understanding how environments select for, or against, plant species is therefore important for managing urban biodiversity and for understanding evolutionary and ecological processes.

Most cities are designed to perform standard functions to meet human needs such as housing, manufacturing, commerce and transportation. Their location is dictated by the need for environmental resources (such as water for drinking and transport and fertile soils for agriculture) (Small & Cohen 2004). Cities are increasingly similar with respect to physical

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structures, materials and open space, resulting in consistent changes to the local physical and biological environment. A common suite of changes, resulting in a common set of conditions, allows urbanization to be considered both as an ecological gradient (McDonnell & Pickett 1990) and as a characteristic suite of disturbances (Sukopp 2004).

We outline a conceptual framework for the assembly of urban floras, including both remnant natural and novel urban environments such as ornamental gardens, roadside verges and parks, based on selective filters. These filters operate generally, with regional factors modifying the relative strength of their effects. The framework permits specific predictions of vegetation response with respect to some commonly measured attributes. We show how this conceptual framework can inform urban ecology research questions and promote a more mechanistic understanding of the effects of urbanization on urban floras.

Conceptual framework for urban floristic change

The pool of plant species found in urban areas is fed from three sources: (a) native species originally present in the area; (b) regionally native species originally absent from the area that colonize novel habitats created by urbanization; and (c) alien species introduced by humans that escape to establish wild populations in urban environments. Urban floras are a subset of the species pool after passage through four filters. These are: (i) habitat transformation, (ii) habitat fragmentation, (iii) urban environmental conditions, and (iv) human preference (Fig. 1). Habitat transformation and fragmentation are anthropogenic filters present in most ecosystems, while the strong influences of human preference and urban environmental conditions are unique to cities.

Each of these filters represents a selection pressure that can leave a signature on urban floras from which we might gain ecological and evolutionary insight. Selection pressures can lead to non-random species gains and losses, changes in species abundances within communities, altered distributions of plant functional traits, and changes to the phylogenetic distribution of species within the urban flora. These filters can also act as agents of natural selection on populations of plants persisting within urban environments (Cheptou *et al.* 2008).

The four urbanization filters (Fig. 1) operate simultaneously as urban centres develop, making it difficult to isolate single drivers of individual species losses or gains. Nevertheless, understanding how individual filters act differentially and select for particular species is important for understanding urban ecosystems. Below we consider how each of the filters could select for the gain or loss of species with certain functional traits, along with trait evolution, in urban environments.

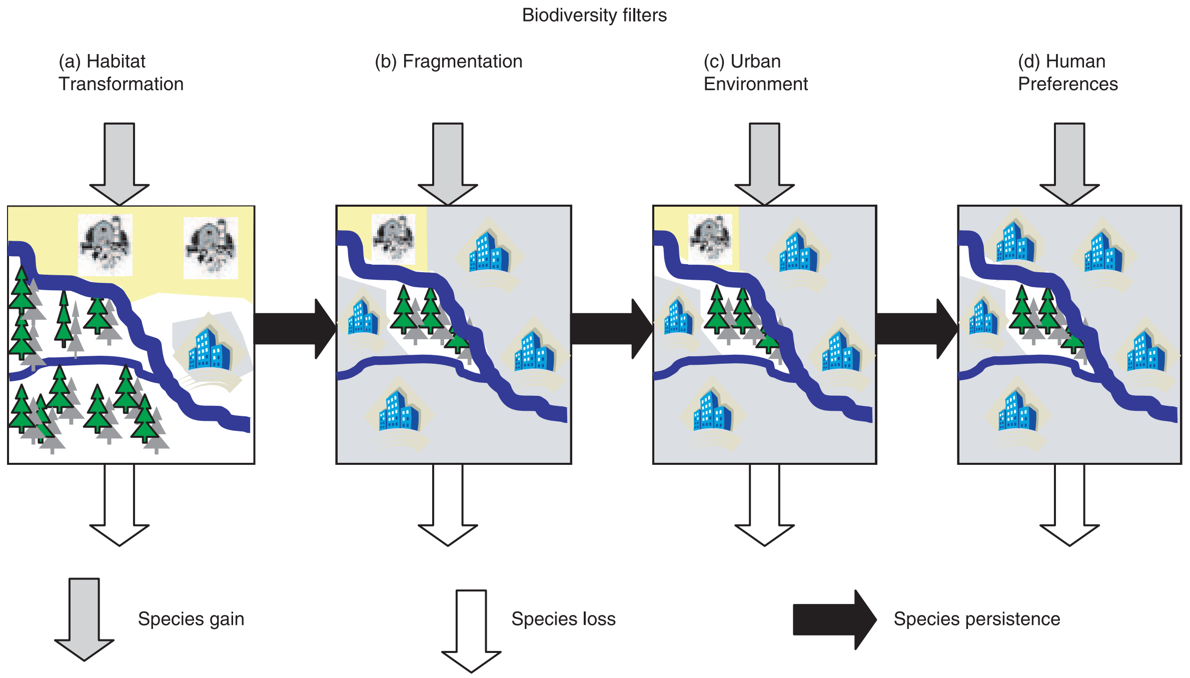

Fig. 1. A schematic model of major urban filters that add (grey arrows) and remove (white arrows) plant species resulting in altered species persistence (black arrows). Urban areas (building icon) may be developed from either native vegetation (tree icon) or agricultural land (farm icon). Panels represent filters of plant diversity that may select on floristic composition, plant functional traits or the phylogenetic structure of communities. Although displayed in temporal sequence; different parts of an urban environment will likely experience each filter at different times, resulting in filters acting simultaneously within the entire urban environment. (a) *Habitat transformation* adds species by creating novel urban environments, and removes species due to the loss of native vegetation. (b) *Fragmentation* removes species that are unable to persist in small isolated areas, which can then be colonized by additional species. (c) *Urban environments* are unlike non-urban environments due to a suite of environmental changes (e.g. pollution, urban heat island) that can select for or against species. (d) *Human preferences* add and remove species. Each filter contributes to a suite of taxa that can persist in urban environments.

Filter 1: habitat transformation

In the United States, only 10–20% of the land area occupied by cities remains as natural habitat (The Heinz Center 2002). If this is typical of cities elsewhere, or even generous relative to older European cities, then species–area relationships predict that many species would be lost simply as a consequence of the transformation and loss of natural habitats (Fig. 1, panel 1). Particular habitats, however, may predictably suffer differential loss due to human preferences (e.g. loss of flat, fertile areas versus retention of escarpments) (Stehlik *et al.* 2007). Furthermore, the history of past land use is likely to influence strongly the extent of species loss following urbanization. Cities that develop within agricultural landscapes are likely to lose fewer species than those that develop in more pristine natural habitats because many vulnerable species would already have been extirpated by habitat transformation associated with agricultural development (Preston 2000). We predict that species loss as a direct result of urban habitat transformation will result in a net loss of species and create a detectable signature on the distribution of plant functional traits and/or on the phylogenetic distribution of the urban flora simply through the selective conversion of particular natural habitats (Table 1). The strength of this filtering signal is likely to differ among cities based on biogeographic setting. For example, wetlands, saltmarshes and mangroves are frequently eradicated from coastal cities and a reduction in the frequency of plant traits associated with these habitats is predicted among coastal cities. Finally, the vulnerability of species to urbanization may differ as a consequence of habitat selectivity. Regions rich in endemic species are often characterized by patchy habitats in which the endemics are concentrated (e.g. serpentines, vernal pools, granitic outcrops). Species losses will depend on the habitat affinities of local endemics relative to patterns of urban development.

Filter 2: habitat fragmentation

Theory predicts that stable metapopulations are more likely to occur in networks of larger, well-connected habitat patches than in small, isolated patches. Remnant habitat patches within cities are usually small and isolated (Stenhouse 2004). Even if species survive habitat loss, they may be highly susceptible to local extinction through effects associated with habitat fragmentation. Habitat fragmentation should select for a predictable suite of species that carry traits related to metapopulation persistence or persistence despite small population size (Fig. 1, panel 2). For example, species with limited dispersal capacity, low seed production, or no seed bank are more vulnerable to loss via failed recolonization. Similarly, species that are heavily dependent on mutualisms (e.g. specialized pollinators, specialized mycorrhizae), or with high inbreeding depression, are at greater risk of loss through fragmentation (Young *et al.* 2000; Pauw 2007). Species losses from fragmentation may be accompanied by replacement by non-native species. We predict that fragmentation will result in net losses of species, simplifying community structure and narrowing plant traits, but potentially broadening the phylogenetic structure of communities in urban remnants (Table 1). We also predict that fragmentation effects may be particularly evident in tropical environments where a high fraction of native species are heavily dependent on biotic interactions for pollination and dispersal (Corlett 2007), leaving them more vulnerable to isolation.

Filter 3: urban environmental effects

Considering only patch size and isolation is often insufficient to explain plant species distributions in fragmented urban landscapes (Williams *et al.* 2006; Godefroid & Koedam 2007), implying that additional filters associated with urbanization play a role. Urban areas are subject to environmental effects that are not present, or are less important, in other fragmented ecosystems (Grimm *et al.* 2008). These include high levels of soil and atmospheric pollution, elevated temperatures due to the urban heat island and increased water stress (Pickett *et al.* 2001; Grimm *et al.* 2008). The particular environmental effects associated with urban areas may have an impact on the occurrence of species in novel anthropogenic habitats as well as on gains and losses of species from natural remnant habitat patches (Fig. 1, panel 3). We predict that novel urban environments will support relatively simple plant communities

	Floristic composition	Functional traits	Phylogenetic distribution
Habitat transformation			
Habitat losses	*Loss*	*Narrowing*	Narrowing
Novel habitat creation	Gain	Broaden	Broaden
Fragmentation			
Extirpations	*Loss*	*Narrowing*	*Narrowing*
Invasions	Gain	Narrowing	Broaden
Urban environs			
Stressors on natural habitats	*Loss*	*Narrowing*	*Narrowing*
Novel urban habitats	Gain	Shift	Broaden
Human preferences			
Introductions	*Gain*	*Shift*	*Broaden*
Eradications	Loss	Narrowing	Narrowing

Table 1. Hypothesized floristic changes associated with urbanization. The three columns represent common response variables that may be measured to assess effects of urbanization on vegetation (composition, functional traits, phylogenetic distribution). Changes predicted for these four response measures are described across the four urban plant filters of our framework (Fig. 1). In each case, we make simple directional predictions of attribute responses to the filter, highlighting in italics the positive or negative directional response that we predict would dominate each filter

characterized by suites of species that are often not found in urban remnants, with traits that can tolerate these conditions (Table 1). These may be from a narrow range of plant families adapted to urban environments. Similarly, we predict that abiotic environmental change and altered disturbance regimes caused by the urban setting will drive remnant habitats toward reduced diversity and simpler community structure, with a narrower suite of plant traits (Williams *et al.* 2005) (Table 1).

FILTER 4: HUMAN PREFERENCE

The urban landscape has often been described using a remnant patch–urban matrix model, but lumping built environments into a single matrix category is simplistic (Zipperer *et al.* 2000; Pickett *et al.* 2001). Urbanization results in loss of natural habitats, but thus creates a set of new anthropogenic habitats (e.g. parks, pavement, gardens and lawns, road and railroad verges, vacant lots, roofs). Plants in these anthropogenic habitats are typically a combination of horticultural plantings and adventive alien species that establish persistent wild populations; these can form distinct urban plant assemblages (Fig. 1, panel 4). Human preference exerts a strong selective pressure on the number and types of alien species introduced to urban habitats and the extent to which these species are actively managed (Hope *et al*. 2003; Martin *et al.* 2004). Because the probability of establishing a wild population is strongly related to propagule pressure, human preference acts as a filter, favouring some species over others. For example, the number of alien trees and tall shrubs in cities has increased through time relative to other life-forms due to widely planted woody ornamentals that have escaped (Celesti-Grapow & Blasi 1998). Because introductions are likely to far outnumber eradications, we predict that human preferences will cause more gains than losses to urban floras, shifting the overall plant trait distribution and broadening the phylogenetic composition of the flora (Table 1).

Research agenda for urban floras

The framework outlined above allows us to conceptualize how urban floras are derived from a pool of available species, both native and alien, via a series of filters. Our ability to test predictions using this framework, however, is constrained. Historical records may provide lists of species gained or lost following urbanization, but it is difficult to assign individual gains or losses to a specific filter. All four filters operate simultaneously and each could contribute to the gain or loss of a particular species. Despite constraints, we believe we can test key predictions derived from the conceptual framework in order to improve our understanding of the ecology of the urban flora.

COMPARISONS AMONG CITIES

Detailed historical lists, available for some cities, provide records of native species that have persisted or been lost, and native and alien species that have colonized following urbanization. If habitat transformation is a key filter, then we expect a positive correlation between the proportion of native habitat lost through urban development and the proportion of native species extirpated. This general prediction can be further refined when data are available on the differential loss of habitats through urbanization. Predicting that fragmentation should lead to further local extinctions and controlling for the amount of remnant native habitat, we then expect higher rates of loss in older cities.

The relative strength of plant trait shifts following urbanization should parallel the above predictions. For example, differential habitat loss should selectively remove species with traits associated with those habitats while native species that persist in progressively older cities should possess traits associated with survival in fragmented or anthropogenic habitats (e.g. good dispersal ability, generalized mutualisms, dormancy attributes). Many of the alien species that colonize urban environments should also possess traits that allow persistence in anthropogenic habitats, including unspecialized pollination, wind dispersal, pollution tolerance, aesthetic appeal and water stress tolerance.

Anthropogenic urban habitats differ markedly from the natural habitats they have replaced. These ecological differences may influence the extent to which native species can colonize novel urban environments (Fig. 1, panel 3) and the strength of different urbanization filters acting on floristic attributes. Cities are also located in different biomes of the world that are likely to have floras that are differentially pre-adapted to persisting in urban environments. We might, for example, predict stronger filtering effects in environments where the natural biome is more different from cities (e.g. those in tropical forest environments *vs.* those in temperate grassland environments). Alternatively, seed dispersal failure may have very different effects in tropical urban environments, where the vast majority of native species have animal vectors, than in temperate regions (Corlett 2007). It is therefore important to consider both the ways in which urbanization filters may act on the urban flora and the extent to which regional environmental variation plays a role in modifying urban floras.

COMPARISONS WITHIN CITIES

Floristic surveys of the distribution of plants along urban–natural gradients should also reveal plant filtering in response to urbanization. In general, highly urbanized areas, such as the city core, are expected to exert greater selective pressure than suburban areas, which tend to have more green space including natural remnants, gardens and parks. Although urban centres and suburban development are confounded by age, urban areas are socially and physically very heterogeneous, differing in their degree of urbanization and hence the strength of the various filters (e.g. remnant habitat area, heat island effects, pollution loads). Plant frequency or abundance data could provide more refined illustrations of plant selectivity across an urban intensity gradient. Similarly, hypotheses related to urban environment selection can be evaluated using temporal trends in abundance or frequency.

Finally, because cities contain novel, edaphically specialized environments (e.g. pavements and roadside verges), we hypothesize that they act as an evolutionary driver of plant functional traits and species diversity via natural selection. Patchily distributed edaphic anomalies are known to diversify floras in other environments (e.g. serpentine endemicity in California (Rajakaruna 2004)), Examples of this have recently emerged in urban areas; that is, *Crepis sancta* responds to strong selection against dispersal in novel urban habitats (pavement cracks) and loses dispersal ability (Cheptou *et al.* 2008). Our understanding of the selection pressures operating in urban environments may benefit from studies that examine trait variation among conspecifics across gradients from natural to urban areas. Depending on the strength of selection, urban centres may drive the diversification of isolated urban plant populations. Assessing plant traits selected by urbanization is the first step toward focusing studies of cities as agents of selection and evolution.

IMPORTANCE OF THE FRAMEWORK

We propose that using a structured framework to conceptualize how urban environments act as agents of selection is the best way to move toward a mechanistic understanding of urban floras. Because people tend to locate cities in regions of high local biodiversity (Cincotta *et al.* 2000; Kuhn *et al.* 2004) there is a need to understand the ways in which urban centres act as biodiversity filters and how we can maximize the retention of urban biodiversity and the ecosystem service it provides. Identifying plant traits that are favoured or lost through urbanization provides a basis for identifying species and habitats likely to be of conservation concern, or conversely plants that may naturalize in urban areas (Thompson & McCarthy 2008). Plants with traits impacted by multiple urban environmental conditions might be selected for more strongly. For example, high rates of nitrogen deposition, altered soil conditions and the loss of mycophagous mammals that disperse fungal spores are likely to disadvantage plants reliant on specific mycorrhizal associations, particularly those of nutrient-poor habitats. This approach will also allow researchers to identify features of the environment that could be manipulated in order to maintain certain trait or species combinations. Such prioritization could help urban planners and managers to decide the relative importance to place on the large number of impacts (Table 1) associated with the four major filters of urbanization (Fig. 1). We have emphasized, however, that urbanization effects on floras may be contingent on the biome or regional setting in which urban centres reside, making broad generalizations difficult. A larger and more representative set of urban flora studies will foster global syntheses (*sensu* Diaz *et al.* 2007) to determine general patterns that may emerge on the relative importance of different filter strengths. Identifying this framework is the first step toward developing a suite of studies that can be synthesized.

The framework outlined here provides a step towards a more mechanistic understanding of urban floras. Although multiple interacting factors make teasing them apart difficult, explicitly recognizing the various environmental factors that filter floras encourages studies to assess the relative strength of these different factors acting on urban floras. Combining a broad comparative approach with detailed studies of particularly well-documented urban environments has the potential to provide a deeper understanding of the development of urban floras. This framework could also be applied to other taxonomic groups. Our proposed research agenda highlights several approaches that should lead to a better understanding of the plant ecology of urban ecosystems as well as guiding the management of urban floras.

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